

Observations of size-related asymmetries in diet and energy intake of rainbow trout in a regulated river

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Synopsis

We examined diet and diel energy intake of rainbow trout, *Oncorhynchus mykiss*, of different lengths captured by electrofishing between 1991 and 1997 in the Lee's Ferry tailwater, Colorado River, below Glen Canyon Dam, Arizona. Trout diets reflected a depauperate food base and indicated limited potential of different fish size-groups to partition food resources. As evidenced by relative stomach volumes of ingested matter, mid-sized and large trout tended to consume more algae than did small fish, suggesting that they consumed diets of lower nutritional quality. An energy intake model indicated that median consumers among mid-sized and large fish generally failed annually to surpass estimated maintenance energy requirements and that median consumers among mid-sized trout failed to meet or exceed maintenance requirements during all seasons. In contrast, median consumers among small trout met or surpassed maintenance energy requirements during most years and in summer. Results support a hypothesis that larger rainbow trout in lotic systems are food-limited more often than smaller fish.

Introduction

Increasing abundance of salmonids in cold dam tailwaters may be paralleled by food base degradation, depression of fish growth, and declining average fish size (Walters & Post 1993, Bohlin et al. 1994, Weiland & Hayward 1997). Trout growth may be influenced by variables such as temperature, diet, and fish population density (Grove et al. 1978, Austreng et al. 1987, Jenkins et al. 1999). Food limitation of growth has been inferred for salmonids in unregulated streams (Cada et al. 1987, Ensign et al. 1990), as well as in regulated rivers (Filbert & Hawkins 1995, Weiland & Hayward 1997). Although stream trout often may be food-limited, size-related asymmetries in growth of fish likely occur (Walters & Post 1993, Filbert & Hawkins 1995, Weiland & Hayward 1997).

Investigations of food limitation of rainbow trout, *Oncorhynchus mykiss*, growth in cold tailwaters have focused on systems with seasonally variable water temperatures (Filbert & Hawkins 1995, Weiland & Hayward 1997). In comparison, the Colorado River below Glen Canyon Dam (GCD), Arizona is cold and nearly stenothermic (Stevens et al. 1997, McKinney et al. 2001b). Relative abundance of rainbow trout in the Lee's Ferry tailwater below GCD increased following implementation of higher minimum and less variable discharges from the dam (McKinney et al. 2001b). During these stabilized flow regimes, relative condition of small fish changed little, whereas condition of larger trout increased initially, then declined (McKinney et al. 2001b), suggesting size-related asymmetries in well-being. The objective of the present study was to examine diet, energy intake, and growth of rainbow trout of different lengths in the Lee's

Ferry tailwater during the stabilized flow regimes of 1991–1997.

Material and methods

Study site

Glen Canyon Dam impounds the Colorado River in northcentral Arizona, and the Lee's Ferry tailwater extends 25.5 km downstream. Mean depth and width, respectively, of the 341 ha tailwater are 6.5 m and 135.6 m at a dam discharge rate of $426 \text{ m}^3 \text{ s}^{-1}$. Non-native rainbow trout are the most abundant fish and coexist with less abundant native flannelmouth sucker, *Catostomus latipinnis*, and nonnative common carp, *Cyprinus carpio*.

The Lee's Ferry rainbow trout fishery is sustained by natural reproduction, although annual stocking of trout ≤ 120 mm by the Arizona Game and Fish Department (AGFD) ranged from 72 000 to 103 000 between 1991 and 1995, then declined to ≤ 25 000 in 1996–1997 (McKinney et al. 2001b). Rainbow trout in the tailwater spawn primarily during winter to early spring and reach sexual maturity at about 300 mm. Relative abundance particularly of wild-spawned rainbow trout in the tailwater increased between 1991 and 1997 (McKinney et al. 2001b). Trout were stocked annually during April–May at various locations throughout the tailwater. Angler harvest generally was less than 5 000 trout annually between 1991 and 1997, harvest of fish 406–558 mm (slot length) was prohibited, and the daily creel limit was two fish outside this length interval (McKinney et al. 2001b).

Field procedures

Detailed electrofishing procedures, sampling locations, and dam releases during the study are presented by McKinney et al. (2001b). We captured rainbow trout in the Lee's Ferry tailwater by electrofishing continually after darkness and before dawn during winter (January–March), spring (April–June), summer (July–September), and fall (October–December) in 1991–1997 ($n = 23$ trips). We used single-pass electrofishing to capture trout in 9–15 randomly selected 0.6 km transects distributed throughout the tailwater. Habitats varied among and within transects, and sampling included pools, riffles, and runs nonselectively. Many relatively small spawning areas occur throughout the tailwater, but none were sampled directly by

electrofishing. Each trip, we randomly subsampled trout > 100 mm long from the total electrofishing catch for stomach content analysis, and we measured total length (TL, mm) and weights (g) of all fish. We also scanned all fish for coded wire tags implanted at the hatchery in all stocked trout since 1992.

We preserved trout stomachs in 10% formalin in the field and identified and measured stomach contents in the laboratory. We measured the volumes of stomach contents (the portion of the gut between the anterior of the esophagus and the pyloric sphincter; Kimball & Helm 1971) with a graduated cylinder and computed relative stomach volume (RGV, ml food m^{-1} ; Filbert & Hawkins 1995) of total contents, *Cladophora glomerata*, and predominant macroinvertebrates (amphipoda, chironomidae). Volumetric techniques provide a representative measure of bulk, but water trapped within stomach contents may cause error in estimates of volume based on displacement, and we attempted to minimize this problem by blotting ingested material on filter paper (Hyslop 1980). We examined stomach contents from trout of different lengths (small fish 152–304 mm; mid-sized fish 305–405 mm; large fish 406–558 mm) to evaluate diet composition, consumption, and energy intake. Length categories were selected for analysis based on the estimated age of small fish (age 1; AGFD unpublished data), length at sexual maturity, and slot length (McKinney et al. 2001b). Trout stomach samples collected during 1994 were lost and unavailable for analyses.

Calculations and statistics

We followed the procedures of Weiland & Hayward (1997) to develop energy intake models for the different length categories of rainbow trout, based on fish with food present in their stomachs. We selected macroinvertebrate prey taxa for analysis according to relative proportions and presumed importance in trout diets (Angradi 1994, McKinney et al. 1999a,b). We excluded *Cladophora* from energy intake models because the alga provides little or no energetic value to trout (Angradi 1994, Bowen et al. 1995, Weiland & Hayward 1997). We predicted dry weights (DW) of *Gammarus lacustris* Amphipoda from volume-dry weight regressions (AGFD unpublished data). We estimated total chironomid dry weight by multiplying their volumes in stomachs times the specific gravity constant (1.05; Filbert & Hawkins 1995) and assuming that dry weight was 10% of wet

weight (Cummins & Wuychek 1971, Hewett & Kraft 1993).

We used relative stomach volume data for trout captured at night to estimate 24 h food consumption (C_{24}). Although amphipod densities in the drift may be highest during the night (McKinney et al. 1999c), preliminary studies in the tailwater evidenced no diel differences in consumption by trout (AGFD unpublished data). Weiland & Hayward (1997) also found no significant differences in food weight in rainbow trout stomachs between samples collected during daylight or night. Although estimations of daily ration based on the entire digestive tract may have provided greater precision than those based on stomach contents (Héroux & Magnan 1996), estimations based on stomach contents have been used widely in food habits studies (Hyslop 1980, Filbert & Hawkins 1995, Weiland & Hayward 1997). Measuring only stomach contents underestimates actual consumption (Elliott & Persson 1978), and we followed Weiland & Hayward (1997) and Hayward & Weiland (1998) in estimating the instantaneous rate of gastric evacuation. We standardized estimates of C_{24} for *Gammarus* and chironomids by fish dry body weight (25% of wet weight; Hewett & Kraft 1993) and assigned energy density values (Joules mg^{-1} DW) derived for these taxa in the Lee's Ferry tailwater (Blinn et al. 1995). We estimated diel energy ingested (E_{24}) by summing individual estimates for *Gammarus* and chironomids. We derived diel maintenance energy requirements (MR; Joules g^{-1} fish body DW day^{-1}) in relation to body weight, water temperature, and ration size (Elliot 1976, Weiland & Hayward 1997). We incorporated water temperatures (United States Bureau of Reclamation unpublished data) in the Lee's Ferry reach at time of stomach collections into energy intake models.

Cold, stenothermic temperatures of the tailwater precluded use of scale analysis to assess growth of trout, and we estimated annual growth rates of stocked trout by plotting TL of individual fish against elapsed time between stocking and capture and fitting logistic growth curves for each stocked cohort. Data for trout RGVs were highly skewed to the left, and we used Kruskal–Wallis tests to determine annual and seasonal differences in relative volumes of stomach contents for the different length categories of fish. Using the arithmetic mean when data are not normally distributed may result in overestimation of daily ration values (Héroux & Magnan 1996). We therefore compared median values of MR and E_{24} stratified by fish length-classes among years and seasons using the Wilcoxon

sign ranks test (Weiland & Hayward 1997). Median values of E_{24} below MR indicated that metabolic costs were not met by consumption, whereas values of E_{24} not significantly different from or significantly greater than MR indicated that median consumption was adequate to allow growth on a given sampling date (Weiland & Hayward 1997).

Statistical power of Kruskal–Wallis tests yielding p values of 0.05 or greater was estimated by using procedures for a parametric one-way analysis of variance. The resulting power estimates were then corrected for efficiency of the Kruskal–Wallis test relative to its parametric analog (95.5%; Daniel 1989, Buchner¹).

Results

We collected 658 rainbow trout 152–550 mm to obtain food habits data (small fish $n = 126$; mid-sized fish $n = 393$; large fish $n = 139$ mm); 21% ($n = 138$) of stomachs were empty. Growth rates were estimated from a subsample of 411 stocked fish. Sample sizes of trout of different lengths for analyzing food habits and estimating median daily energy intake varied annually and seasonally (Table 1). *Cladophora*, *Gammarus*, and chironomids together accounted for more than 90% of stomach content volume, and *Gammarus* and chironomids comprised more than 90% of animal matter by volume. Young fishes rarely enter the tailwater from the reservoir, and fish eggs or remains comprised less than 1% by volume.

No clear differences in diet content or consumption (RGV) were apparent for small fish among years, but statistical power resulting from this sample size was generally low (0.07–0.77). Diet composition appeared to be similar for small, mid-sized, and large fish, but consumption by mid-sized trout differed among years (Figure 1). Total RGV differed ($H = 16.0$, $df = 5$, $p = 0.01$) between 1991 and 1997, and the RGVs for *Gammarus* and *Cladophora* increased, but RGVs for chironomids declined, during this period ($H \geq 11.4$, $df = 5$, $p \leq 0.04$), for mid-sized trout. The RGV for *Cladophora* for large trout also tended to increase among years ($H = 10.0$, $df = 5$, $p = 0.07$).

Diet composition was similar among seasons, and total RGV tended to be greater in summer, for all length-groups, but length-specific seasonal differences

¹ Buchner, A., E. Erdfelder & F. Faul. 1997. How to use G*Power. URL [http://www.psychologie.uni-trier.de:8000/projects/g\[pwer/how_to_use_gpower.html](http://www.psychologie.uni-trier.de:8000/projects/g[pwer/how_to_use_gpower.html).

Table 1. Annual and seasonal sample sizes for rainbow trout of different lengths captured by electrofishing, Lee's Ferry tailwater, Colorado River.

	1991	1992	1993	1995	1996	1997
Annual						
152–304 mm	4	15	27	23	23	34
305–405 mm	33	19	22	80	137	102
406–558 mm	29	20	16	11	24	39
Winter						
152–304 mm	2	0	11	0	12	0
305–405 mm	20	0	8	0	14	0
406–558 mm	18	0	5	0	2	0
Spring						
152–304 mm	2	0	9	10	5	7
305–405 mm	13	3	6	26	13	30
406–558 mm	11	6	8	7	1	14
Summer						
152–304 mm	0	9	4	0	5	13
305–405 mm	0	9	5	0	52	51
406–558 mm	0	5	2	0	9	15
Fall						
152–304 mm	0	6	3	13	1	14
305–405 mm	0	7	3	54	58	21
406–558 mm	0	9	1	4	12	10

in consumption were apparent (Figure 2). The RGV for *Gammarus* peaked significantly during summer only for mid-sized fish ($H = 14.2$, $df = 3$, $p \leq 0.01$), whereas chironomid RGV was greatest in spring for small fish and in summer for mid-sized trout ($H \geq 8.3$, $df = 3$, $p \leq 0.05$). The RGV for *Cladophora* was greater during summer than other seasons for mid-sized and large trout but was greater during spring and summer for small fish ($H \geq 14.6$, $df = 3$, $p \leq 0.01$). The RGVs for the alga for small, mid-sized, and large trout, respectively, were $28.3 (\pm 7.8 \text{ SE})$, $35.5 (\pm 4.2 \text{ SE})$, and $46.8 (\pm 8.2 \text{ SE})$ percent of total RGVs for these size groups during summer.

Estimated annual growth of small stocked trout (<305 mm TL at capture) ranged from 80 to 207 mm, whereas annual growth of mid-sized and large fish ranged from 10 to 63 mm (Figure 3). Sample sizes for estimating growth were: 1992 cohort $n = 87$; 1993 cohort $n = 182$; 1994 cohort $n = 103$; 1995 cohort $n = 39$. The exponent of the logistic growth equation (intrinsic growth rate) for stocked cohorts was greatest for trout stocked in 1995, intermediate for those stocked in 1993 and 1994, and lowest for fish stocked in 1992. Stocked trout generally reached a maximum of about 350 mm TL after three years of residence in the system, although greater growth by this age may have occurred for the 1995 cohort.

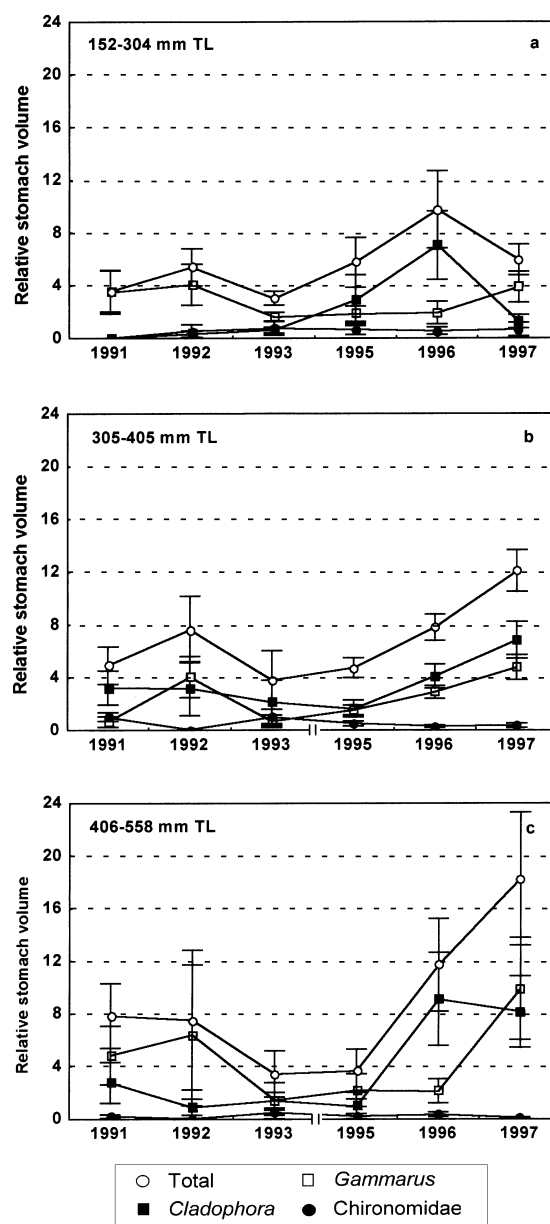


Figure 1. Mean (\pm SE) annual total, *Gammarus*, *Cladophora*, and chironomidae relative stomach volumes (RGV) of rainbow trout of different lengths (a–c), Lee's Ferry tailwater, Colorado River.

Median daily energy intake by small trout met or exceeded maintenance energy requirements during 1991, 1992, and 1997 (Figure 4). Median consumers among mid-sized trout did not meet or exceed maintenance energy intake levels during any year ($Z \geq 2.4$, $n \geq 15$, $p \leq 0.02$), and median consumers

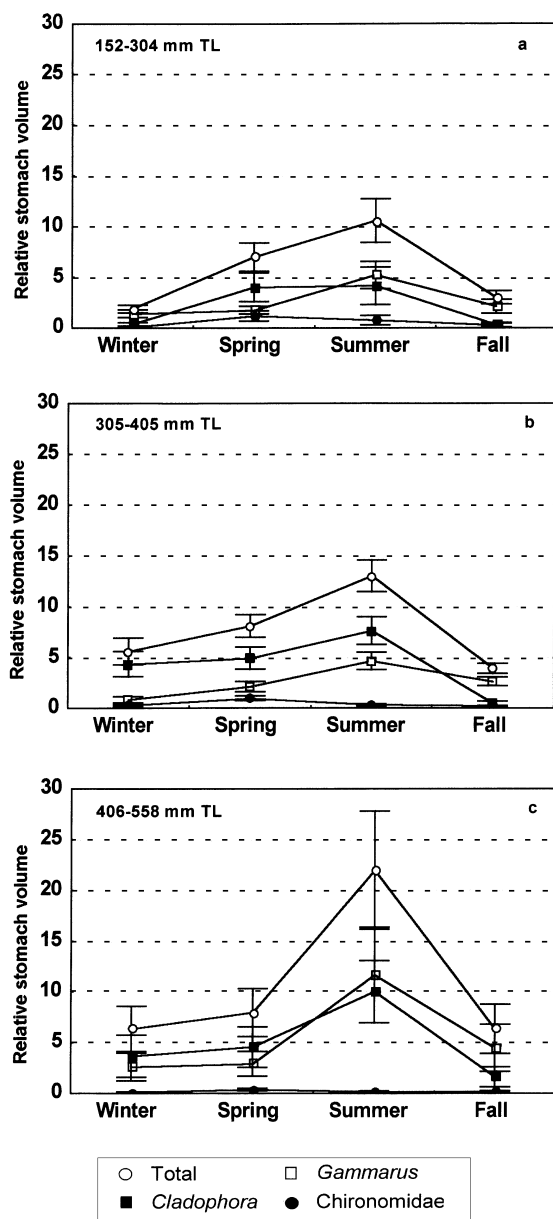


Figure 2. Mean (\pm SE) seasonal total, *Gammarus*, *Cladophora*, and chironomidae relative stomach volumes (RGV) of rainbow trout of different lengths (a–c), Lee’s Ferry tailwater, Colorado River, 1991–1997.

among large trout did not meet maintenance energy requirements during any years except 1992 and 1997 ($Z \geq 2.5$, $n \geq 10$, $p \leq 0.01$). Median diel energy ingested by small and large trout also met or exceeded maintenance energy requirements during summer, but median diel energy intake by mid-sized fish did not

meet MR during any season ($Z = 3.8$, $n \geq 26$, $p \leq 0.01$; Figure 5). Percentages of estimated maximum daily consumption (C_{\max}) among length-groups were: 152–304 mm = 30.2%; 305–405 mm = 20.7%; 406–558 mm = 29.4% ($H = 13.7$, $df = 2$, $p \leq 0.01$).

Discussion

Our results suggest that poorer energetic conditions existed among median consumers for mid-sized and large, as compared to small, rainbow trout in the Lee’s Ferry tailwater and that growth of median consumers among mid-sized and large fish was food-limited. Growth rates of trout in the tailwater are also likely suppressed by the cold, nearly stenothermic water temperatures associated with hypolimnetic releases from the reservoir (Hokansen et al. 1977, Jobling 1981, Austreng et al. 1987). Mainchannel water temperatures were similar annually and ranged between 8.4 and 9.5°C (McKinney et al. 2001b). Variations within this temperature range likely had comparatively little effect on consumption by trout (Elliott 1975, Storebakken & Austreng 1988), growth (Edwards et al. 1979, Austreng et al. 1987), or efficiency of food utilization (Cho 1992).

Harvest of trout changed little during the present study, whereas relative abundance increased, and condition of mid-sized and large fish declined after 1994 (McKinney et al. 2001b). In comparison, diet composition showed little change during the study, and energetic conditions for mid-sized and large trout generally were poor. However, reduction in annual stocking rates by at least 65% after 1995 was followed by greater relative abundance of wild-spawned trout in 1997 (McKinney et al. 2001b) and may have been associated with increased growth and improved energetic conditions. The energy intake model generally agreed with differences in relative condition observed between small and mid-sized or large fish captured in the tailwater (McKinney et al. 2001b).

Our estimates of diel ingested energy incorporated only *Gammarus* and chironomids and therefore are biased conservatively. Due to minimal energetic value to trout (Angradi 1994, Bowen et al. 1995, Weiland & Hayward 1997), we eliminated *Cladophora* and its epiphytes from our energy intake model. Conversely, *Gammarus* and chironomids are the predominant macroinvertebrate prey of rainbow trout in the Lee’s Ferry tailwater (McKinney et al. 1999a,b) and provide nutritional value (Mathias et al. 1982, Angradi 1994, Weiland & Hayward 1997), although food quality of

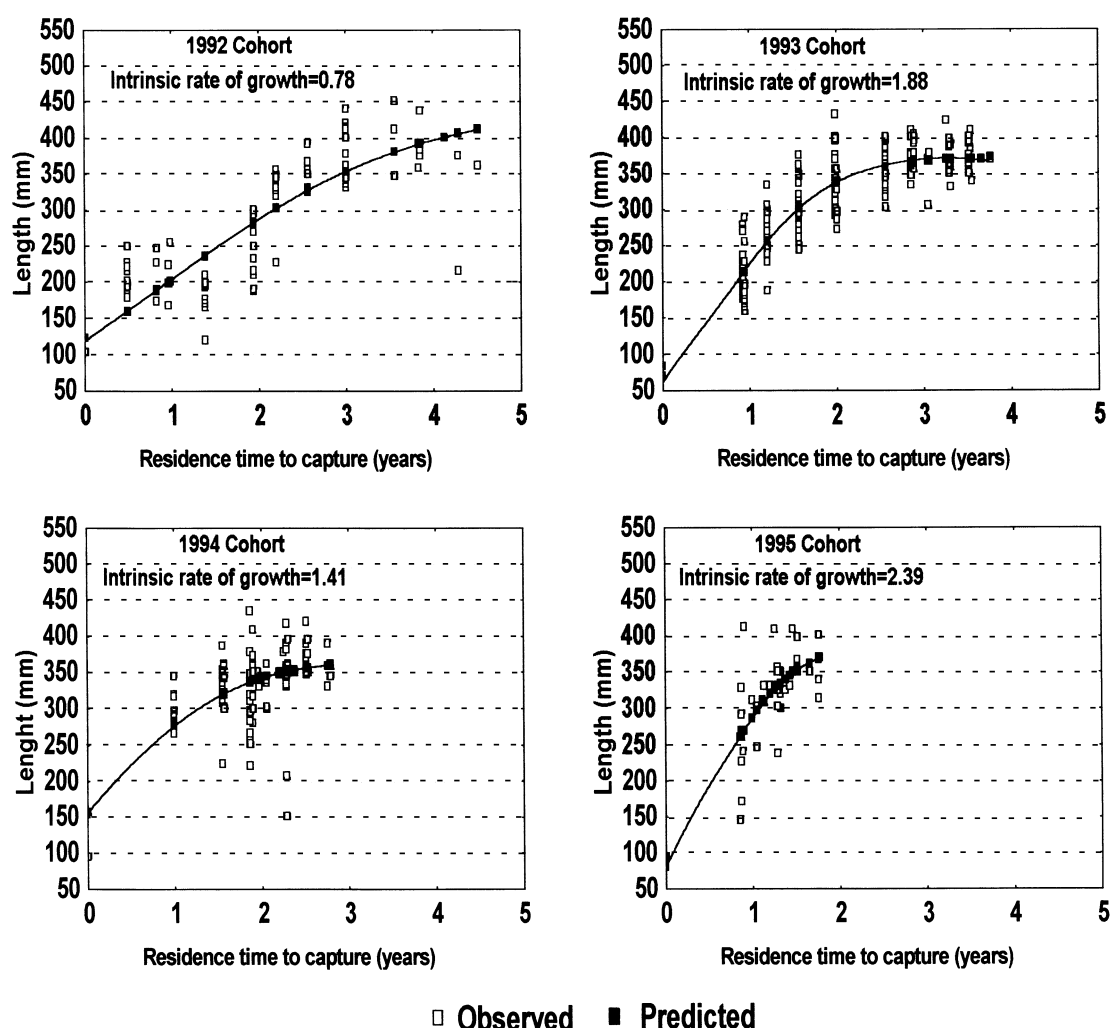


Figure 3. Observed and predicted logistic growth models of stocked rainbow trout cohorts, Lee's Ferry tailwater, Colorado River, 1991–1997.

chironomids may be lower than that of *Gammarus* (Hayward & Weiland 1998).

Similarity of diet composition in the tailwater among years and seasons for the different length-classes of rainbow trout reflected the depauperate aquatic food base in the tailwater (Blinn et al. 1995, Stevens et al. 1997, McKinney et al. 1999c) and indicated that these trout may not partition food resources. However, *Cladophora* comprised a larger proportion of stomach contents of mid-sized and large than of small trout, and RGVs of the alga indicated that diet in general tended to be relatively poor (Weiland & Hayward 1997). Total consumption and consumption of *Cladophora*

and *Gammarus* by large, and particularly mid-sized fish, increased over years, suggesting compensatory feeding and low nutritional quality of the diet (Lee & Putnam 1973, Grove et al. 1978, Bowen et al. 1995, Weiland & Hayward 1997), and poor nutritional quality may have contributed to lessened growth of mid-sized and large fish (Weiland & Hayward 1997).

Consistent with our findings that median consumers particularly among mid-sized trout in the tailwater were food-limited, relative condition of mid-sized fish declined following sudden reductions in releases from the dam that were associated with dramatically lowered benthic macroinvertebrate densities

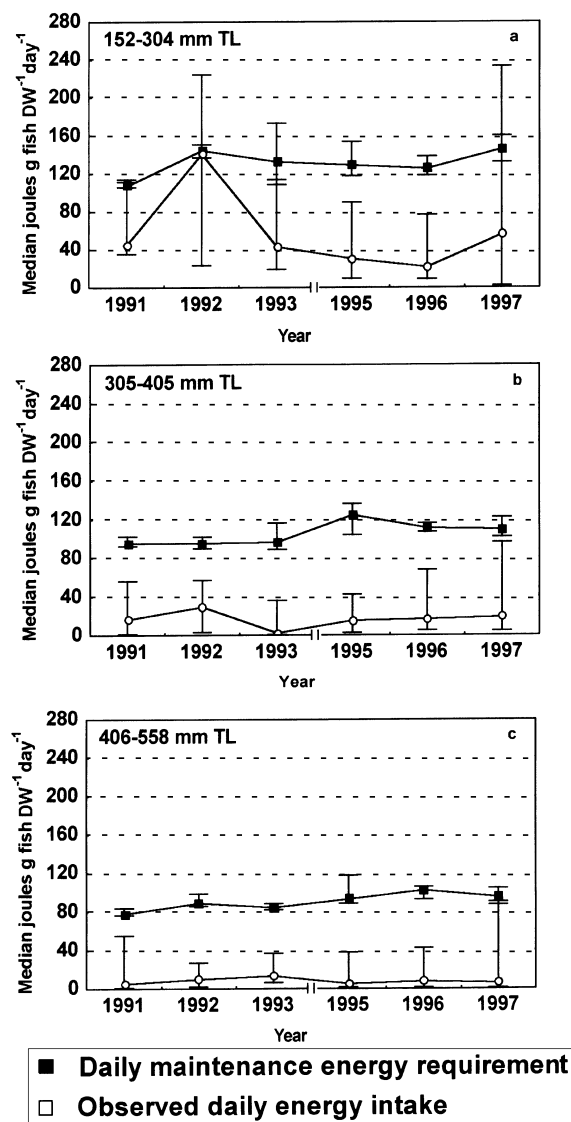


Figure 4. Annual median (bars indicate 25th and 75th percentiles) estimated daily energy intake and maintenance energy requirements for rainbow trout of different lengths (a-c), Lee's Ferry tailwater, Colorado River, 1991-1997 (DW = dry weight).

(McKinney et al. 1999b). Compared to smaller fish, larger rainbow trout in the tailwater also evidenced greater infestation by a parasitic gut nematode (McKinney et al. 2001a) that might impair growth (Hiscox & Brocksen 1973).

Moreover, mean macroinvertebrate drift densities in the tailwater during 1993 and 1994 (McKinney et al. 1999c) were one-third or less than those reported for the regulated Green River, where growth of rainbow

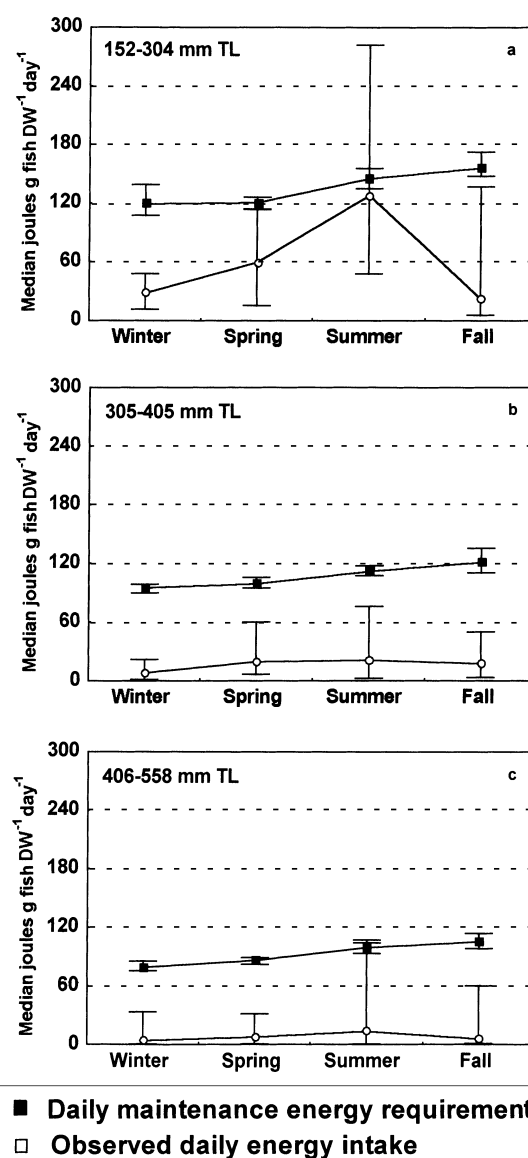


Figure 5. Seasonal median (bars indicate 25th and 75th percentiles) estimated daily energy intake and maintenance energy requirements for rainbow trout of different lengths (a-c), Lee's Ferry tailwater, Colorado River, 1991-1997 (DW = dry weight).

trout was limited by food and temperature (Filbert & Hawkins 1995), suggesting comparatively low prey availability in the Lee's Ferry reach. However, water temperatures were much higher in the Green River, at least during summer to fall, than in the Lee's Ferry tailwater (Filbert & Hawkins 1995), suggesting that maintenance energy requirements were lower in the

Colorado River. Maintenance energy requirements for rainbow trout may be more than 50% lower at 7.5°C than at 15°C (Cho & Kaushik 1990, Cho 1992). Similar to other findings associated with food limitation of trout growth (Weiland & Hayward 1997), consumption rates for all length-groups tended to be low relative to the maximum consumption potential, although consumption by mid-sized trout was proportionally less than that of small or large fish.

Seasonally, water temperatures in the Lee's Ferry reach increased from a low of 8.2°C in spring to a high of 10.2°C in fall (United States Bureau of Reclamation unpublished data). Nonetheless, trout in the tailwater tended to increase consumption during summer, as indicated by relative stomach volumes of total ingested matter, *Gammarus*, and *Cladophora*, and by diel energy intake estimates. This seasonal trend in consumption is similar to that observed in other cold tailwaters with more variable water temperatures (Filbert & Hawkins 1995, Weiland & Hayward 1997).

In general, body size of salmonids tends to decline with increased population densities (Bohlin et al. 1994), and relative abundance of rainbow trout in the Lee's Ferry tailwater increased more than threefold between 1992 and 1997 (McKinney et al. 2001b), consistent with an expectation of density-dependent changes in growth. If our estimates of median diel energy intake approximate actual levels in the population, comparatively few mid-sized or large fish met or surpassed maintenance energy levels, indicating poorer energetic conditions for larger than for smaller trout. In comparison to mid-sized and large fish, median consumers among small trout in the tailwater tended to meet or surpass maintenance energy requirements more often, and small trout generally evidenced greater relative condition (McKinney et al. 2001b). However, only mid-sized rainbow trout consuming energy at median levels did not meet or exceed maintenance energy requirements in any year or season, whereas median consumers among large fish met or exceeded maintenance energy requirements in summer but not in most years. Filbert & Hawkins (1995) also found that medium-sized rainbow trout (300–350 mm) showed the strongest response to changes in the food-temperature gradient, whereas smaller (200 mm) fish changed little in response to this gradient. High seasonal drift of amphipods (McKinney et al. 1999a) coincident with size-related behavioral advantages (Fausch 1984, McCarthy et al. 1992) may have contributed to better energetic conditions during summer for large as compared to mid-sized trout.

Genotype of the fish, food availability, and water temperature are important variables influencing the potential for growth (Wootton 1982). Growth rates of fishes tend to decline beyond some point of inflection as individuals become older (Ricker 1979, Wootton 1982, Jobling 1983, Fruend & Littel 1991), as we observed for stocked rainbow trout in the Lee's Ferry tailwater. The Bel Aire strain of farmed trout (Crystal River Hatchery, Colorado) in our study has been stocked annually in the tailwater since 1986 and appears to be well-adapted to local conditions (AGFD unpublished data). Some stocked trout in our study survived for more than four years.

We believe that growth of mid-sized and large rainbow trout in the Lee's Ferry tailwater was limited in part due to cold-stenothermic conditions of the reach but also because allocation of the limited available energy among median consumers was devoted to metabolism and reproduction. Large fish may allocate more energy to reproduction than somatic growth, consistent with our finding that natural recruitment into the population was high (McKinney et al. 2001b) but that growth of large fish was comparatively slow, and few trout grew to more than 405 mm long. Under laboratory conditions, the thermal optimum for growth of rainbow trout is about 17–18°C (Hokansen et al. 1977, Jobling 1981). Water temperatures in the Green River below Flaming Gorge Dam in Utah may be about 15°C during late summer to early fall (Filbert & Hawkins 1995). Rainbow trout stocked at 100 mm in the Green River tailwater may exceed 250 mm in a year's time (Wiley & Dufek 1980). In contrast, stocked trout in the Lee's Ferry tailwater, generally grew only about 230 mm to a length of 350 mm after three years of residence, considerably less than the management recommendation that the tailwater produce fish 457 mm long by age-3 (AGFD unpublished). Although maintenance energy requirement per kg of body weight is higher for small than large fish, the energy cost of production is higher for large fish (Cho 1992), and larger trout may require a broader size-spectrum of prey than is available in the Lee's Ferry tailwater.

We suggest that incorporating diet data for rainbow trout into energy intake models (Weiland & Hayward 1997) is applicable to management-related investigations and can supplement routine food-habit studies. Our findings and those of others (Elwood & Waters 1969, Cada et al. 1987, Ensign et al. 1990, Filbert & Hawkins 1995, Weiland & Hayward 1997) support a hypothesis that larger salmonids in lotic systems may be food-limited more often than smaller fish. Although

cold and nearly stenothermic releases from the dam may preclude greater diversity of the prey base for rainbow trout in the Lee's Ferry tailwater (Stevens et al. 1997), greater amphipod densities and prey assemblages with broader size-spectra might enhance conditions for growth of trout (Weiland & Hayward 1997).

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